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# The bright zone, a specialized dorsal eye region in the male blowfly *Chrysomyia megacephala*

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**Summary.** 1. In the compound eye of the male *Chrysomyia megacephala* the facets in the ventral part of the eye are only ca. 20 μm in diameter, but increase abruptly to ca. 80 μm above the equator of the eye. Correspondingly there is a large and abrupt increase in the rhabdomere diameter from 2 to as much as 5 μm. The far-field radiation pattern of the eye shows that, despite the large change in ommatidial dimensions, the resolution of the eye remains approximately constant across the equator: angular sensitivity of the photoreceptors and sampling raster are similar ventrally and dorsally. The main result of the large dorsal facets is a more than tenfold increase in light capture. Thus this eye provides a clear example of an insect where large dorsal facets have evolved not for higher acuity, but rather for higher light capture.

2. Sensitivity is increased even more by a seventh photoreceptor cell joining neural superposition, as reported before for the dorsal eye of male houseflies. All seven photoreceptors have the same spectral sensitivity.

3. Angular sensitivities in the dorsal eye are more Gaussian-shaped than the flat-topped profile expected for large rhabdomere diameters. This is explained by the anatomical finding that the dorsal rhabdomeres taper strongly. It is suggested that the combination of high photon capture and rounded angular sensitivities is advantageous for monitoring movement and position of small objects.

4. Finally some of the constraints involved in constructing specialized dorsal eye regions for detection of small objects are considered.

*Abbreviation: LMC* large monopolar cell

## Introduction

Sexual dimorphism of the eyes is a striking property of many insect species (Dietrich 1909; Collett and Land 1975; Kirschfeld and Wenk 1976; Beersma et al. 1977; Franceschini et al. 1981; Zeil 1983a; revs. Land 1981a; Wehner 1981). An extreme case is the mayfly where the males have excessively enlarged dorsal eyes, referred to as turbanate eyes (e.g. Wolburg-Buchholz 1976; Horridge and McLean 1978). The males of many dipterans also have greatly enlarged eyes; sometimes to such an extent that, as in the mayfly, dorsal and ventral eyes are separated by a band (for references see Wehner 1981). Such turbanate, or divided eyes are typically found in swarming species such as simuliids (Kirschfeld and Wenk 1976; Kirschfeld 1979) and bibionids (Zeil 1979, 1983a) where the greatly enlarged dorsal eyes of the males with their large facets can view females flying above them against the sky.

Even though such a striking separation of dorsal and ventral eye halves is not usually apparent in the more common higher flies such as hoverflies, houseflies and blowflies, there is still often a distinct sexual dimorphism in eye structure. In particular, the eyes of the male are usually larger, and the two eyes often meet dorsally. The region of enhanced vision, however, is now usually looking in a frontal-dorsal direction (Collett and Land 1975; revs. Stavenga 1979; Wehner 1981; Land 1981a; Hardie 1985). In these cases as well, the specialized dorsal eye regions are associated with higher acuity and are often referred to as foveae or, more descriptively, 'acute zones' (Horridge 1978; Wehner 1981; Land and Eckert 1985).

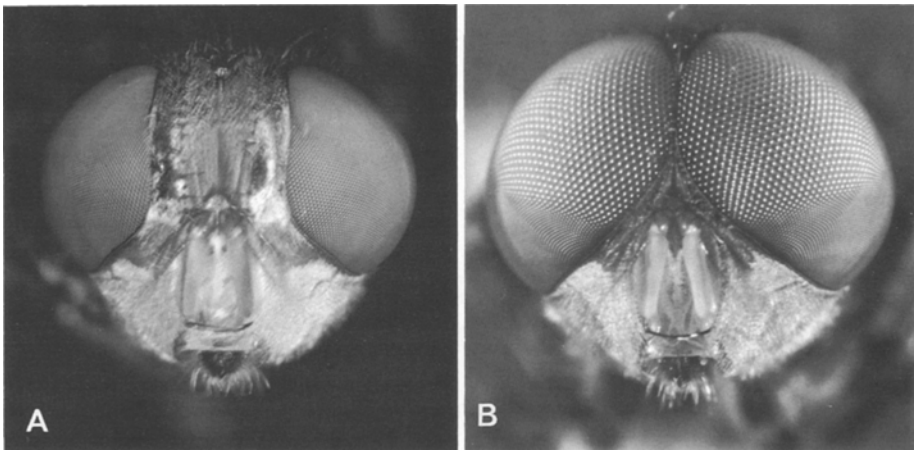


**Fig. 1.** Female (**A**) and male (**B**) *Chrysomyia*. The greatly enlarged facets in the dorsal eye of the male can be clearly seen

Behavioural observations suggest that the large dorsal eyes allow for the ready detection and/or tracking of potential mates (Kirschfeld and Wenk 1976; Kirschfeld 1979; Zeil 1983b; rev. Wehner 1981). This behaviour has been best studied in hoverflies (Collett and Land 1975) and houseflies (Wehrhahn and Hausen 1980). In houseflies, the sexual dimorphism apparent at the level of the cornea has been shown to persist in the shape of sex-specific photoreceptors and interneurones in successive neuropils of the visual system, including the retina (Franceschini et al. 1981; Hardie et al. 1981), the lamina (Hardie 1983) and the lobula (Hausen and Strausfeld 1980).

Recently we started to investigate the blowfly *Chrysomyia megacephala*, a calliphorid species found throughout Asia where it is regarded as a pest because the females lay their eggs in drying fish. The males of this species have unusually large eyes (which in fact give rise to the scientific name), and in particular the size of the facets in the dorsal eye region is huge compared to the facet size ventrally. This marked sexual dimorphism, which is clearly visible with the naked eye, prompted a closer look at the optical characteristics and design principles of the eyes of this male fly. Surprisingly, we found that it is not the angular resolving power of the dorsal eye which is increased, but rather the brightness of the retinal image, and hence our description of this eye region as a 'bright zone'.

## Methods

*Preparation.* Males of the fly *Chrysomyia megacephala* were taken from a laboratory culture. They were fixed with wax and mounted on a goniometer. Care was taken not to impair respiration. A light guide was inserted in a small hole at the back of the head capsule, through which antidromic light propagated through the eye. For electrophysiology a small piece of cornea was removed, and a microelectrode inserted.

*Optical setup.* The setup was similar to the one described in van Hateren (1984, 1985). In this setup the far-field radiation pattern of the eye can be both observed and stimulated. The far-field radiation pattern is the light pattern emerging from the eye towards infinity, usually observed in the focal plane of a lens in front of the eye (see Franceschini 1975). A useful interpretation of the far field is that it shows the way in which the photoreceptor array sees the world (though this is only strictly true for monomodal photoreceptors, as discussed in van Hateren 1984). Far-field radiation patterns of single ommatidia can be observed by selecting a single facet with a diaphragm at an enlarged image of the cornea (van Hateren 1984). Figure 3 was obtained using a water-immersion objective (corneal neutralization, Franceschini 1975).

*Electrophysiology.* Conventional glass electrodes were used, filled with a mixture of 3 *M* KAc and 0.05 *M* KCl, and having typical resistances of 150–200 M$\Omega$. Angular sensitivities of photoreceptor cells were measured by scanning the far field of the eye with a point light source (a light guide with an aperture of 0.2°). The response of the cells to flashes of light was clamped at 6 mV by feedback through a motor-driven neutral density wedge (Smakman and Pijpker 1983; Smakman et al. 1984). The position of the neutral density wedge provides a direct measure of the sensitivity of the cell.

The same clamping method was used for measurements of the spectral sensitivity of photoreceptors (Franceschini 1979). The point light source was then set in the centre of the cell's receptive field. Different wavelengths were produced with broad band K filters (Balzers), having a band-width of approximately 50 nm. Large Monopolar Cells (LMCs) in the lamina were identified from their transient hyperpolarising responses. They were clamped at $-1.5$ mV for measurement of their spectral sensitivity.

Electrophysiology combined with corneal neutralization (van Hateren 1986, 1987) was not feasible for lamina recordings from the dorsal eye, because its shape did not leave enough space for the microelectrode between the cornea and water-immersion objective.

*Anatomy.* Standard EM procedures were followed (e.g. Ribi 1978). Eyes complete with optic lobes and brains were dissected out and fixed in 2.5% formaldehyde plus 2.5% glutaraldehyde in phosphate buffer. After post-fixation in 2% $OsO_4$ the eyes were dehydrated through an alcohol series and embedded in araldite. Semi-thin sections for light microscopy were stained with methylene blue, and ultrathin sections were stained with uranyl acetate and lead citrate.

## Results

### *Optics and anatomy*

*Facet and rhabdomere diameters.* Figure 1 shows the eyes of a female and a male *Chrysomyia*. The enormously enlarged facets in the male dorsal eye are clearly visible. The texture and colour of the ventral and dorsal halves of the male eye differ significantly, the dorsal half being redder than the ventral half. In contrast, the female eye shows no such difference. Figure 2 shows the cornea of a male *Chrysomyia megacephala* seen with antidromic light, at the equator of the eye. The facet diameter increases from about 20 μm ventrally to up to 80 μm dorsally, with an abrupt change one or two rows above the equator (defined as the line about which the trapezoidal rhabdomere patterns are reversed – Fig. 3A). The region of enlarged facets is roughly triangular, each side of the triangle comprising some 20–25 facets. Although the area dominates the dorsal eye half, it is in fact surrounded by 10–25 rows of smaller facets both laterally and dorsally.

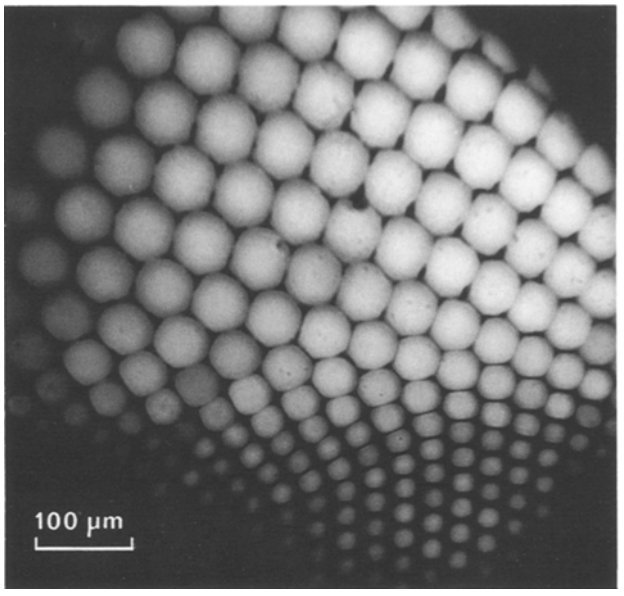


**Fig. 2.** Photograph of the male cornea viewed with antidromic light. Below the equator of the eye the facets are small (about 20 μm), whereas they become much larger above the equator (up to 80 μm)

Not only the facet lenses, but also the underlying rhabdomeres increase dramatically in size above the equator of the eye. This is shown in Fig. 3A, where the ommatidia are observed through a water-immersion objective (corneal neutralization, see Franceschini 1975), thus allowing direct observation of the rhabdomere tips. The large diameter of the dorsal rhabdomeres is confirmed in tangential sections of the ommatidia (Fig. 4). The diameters of the distal part of all 7 rhabdomeres in the specialized region of the dorsal eye range between 3 and 5 μm (Fig. 4A), whilst in the ventral eye the six peripheral rhabdomeres (R1–6) are ca. 2 μm in diameter, and the central rhabdomere (R7) only ca. 1 μm.

Corresponding to the increase in facet and rhabdomere diameter, the focal length of the lenses

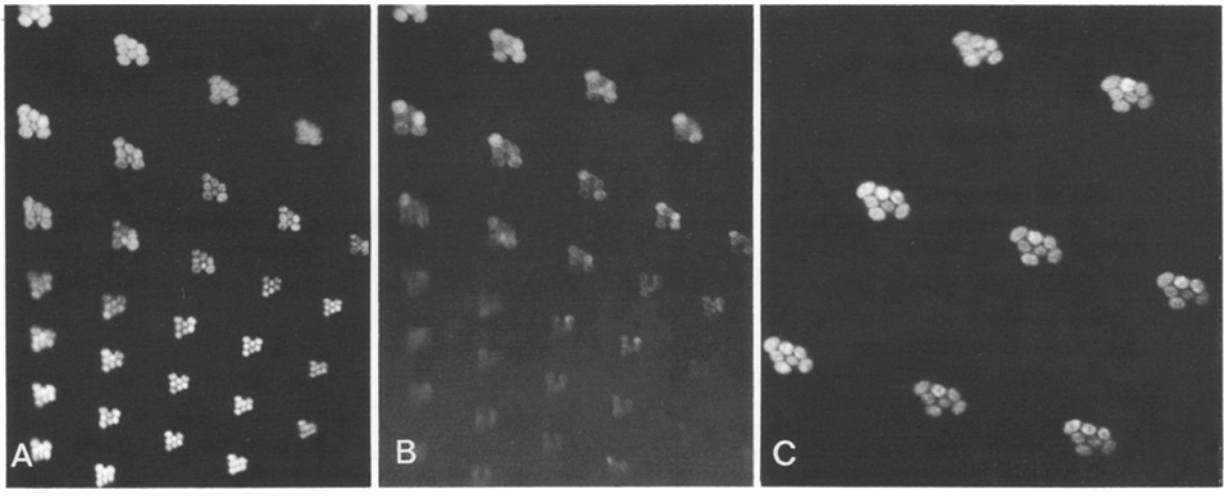


**Fig. 3A–C.** Retina of male *Chrysomyia* viewed with antidromic light and corneal neutralization: a water-immersion objective neutralizes the cornea almost completely, allowing direct observation of the underlying rhabdomeres. **A** Retina below and above the equator (note the mirror-symmetry of the rhabdomere patterns at both sides of the equator) seen at a wavelength of 600 nm. Ventral rhabdomeres are small and monomodal (only $LP_{01}$), dorsal rhabdomeres have larger diameters and show higher order modes. **B** Same as **A**, with $\lambda = 450$ nm. Second order modes ($LP_{11}$) can be seen in ventral rhabdomeres, third and higher order modes in the dorsal ones. **C** More dorsally than **A** and **B**, $\lambda = 600$ nm

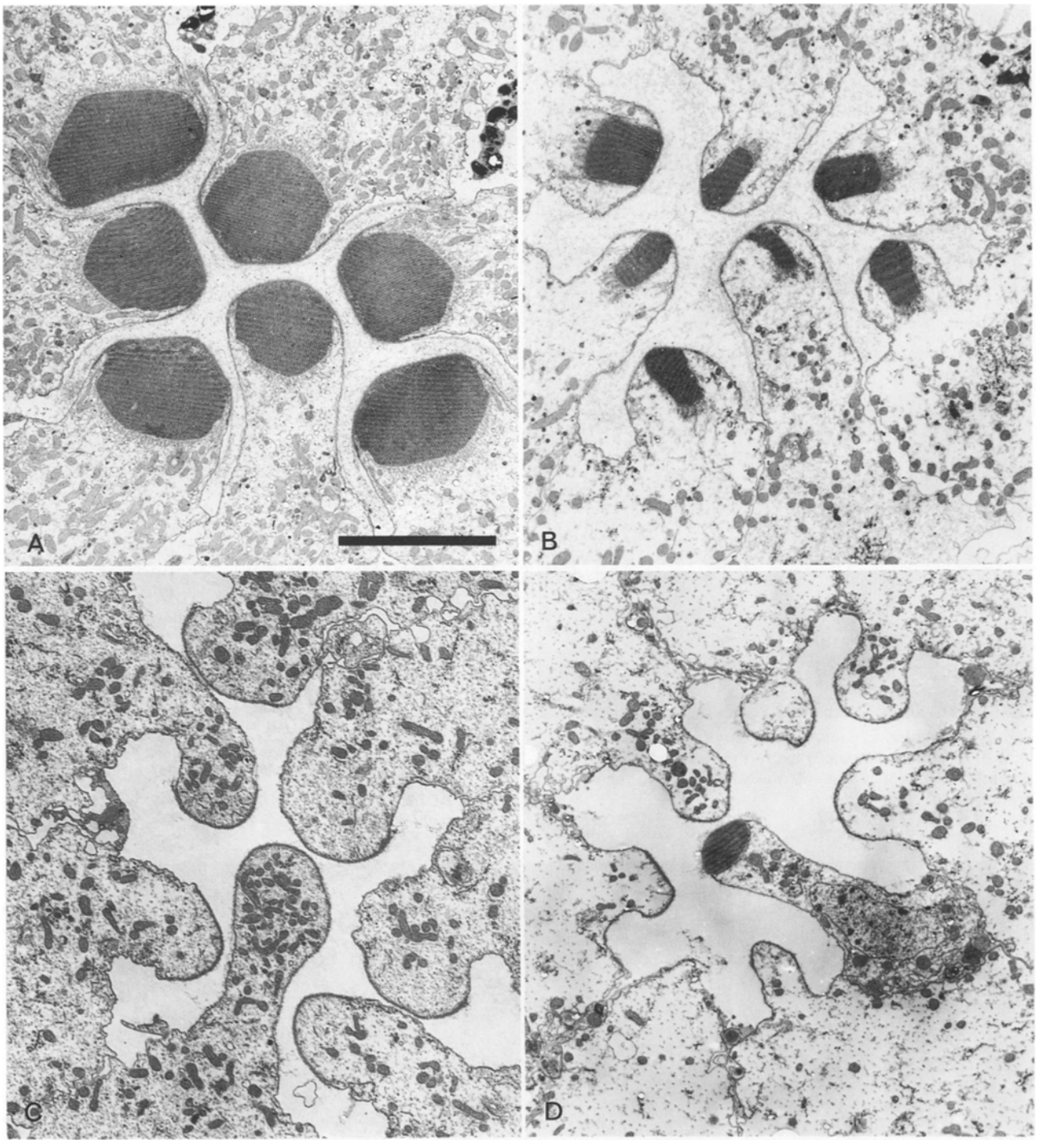


**Fig. 4A–D.** Transmission electronmicrographs of tangential sections through different levels of ommatidia in the male dorsal eye. All sections are from the region of enlarged facets, but not necessarily from the same eye. Depths are approximate only and with reference to the distal tips of the rhabdomeres. **A** 0 μm: a distal section showing the greatly enlarged rhabdomeres. **B** ca. 100 μm deep: the rhabdomeres have tapered greatly. **C** ca. 150 μm deep: no rhabdomeres are observed. **D** Shortly before the basement membrane (ca. 300 μm deep) the rhabdomere of R8 appears. Scale bar: 5 μm

also increases. Whereas in the ventral eye the rhabdomere tips lie ca. 60 μm behind the lenses, in the specialized dorsal region this value increases to ca. 150 μm. Optical measurements on isolated corneas (Stavenga et al., in preparation) show that in all eye regions there is a more or less constant F-number of ca. 2.0; the effective F-number will be slightly larger due to the aperture formed by the primary pigment cells.

A surprising finding in successively deeper tan-

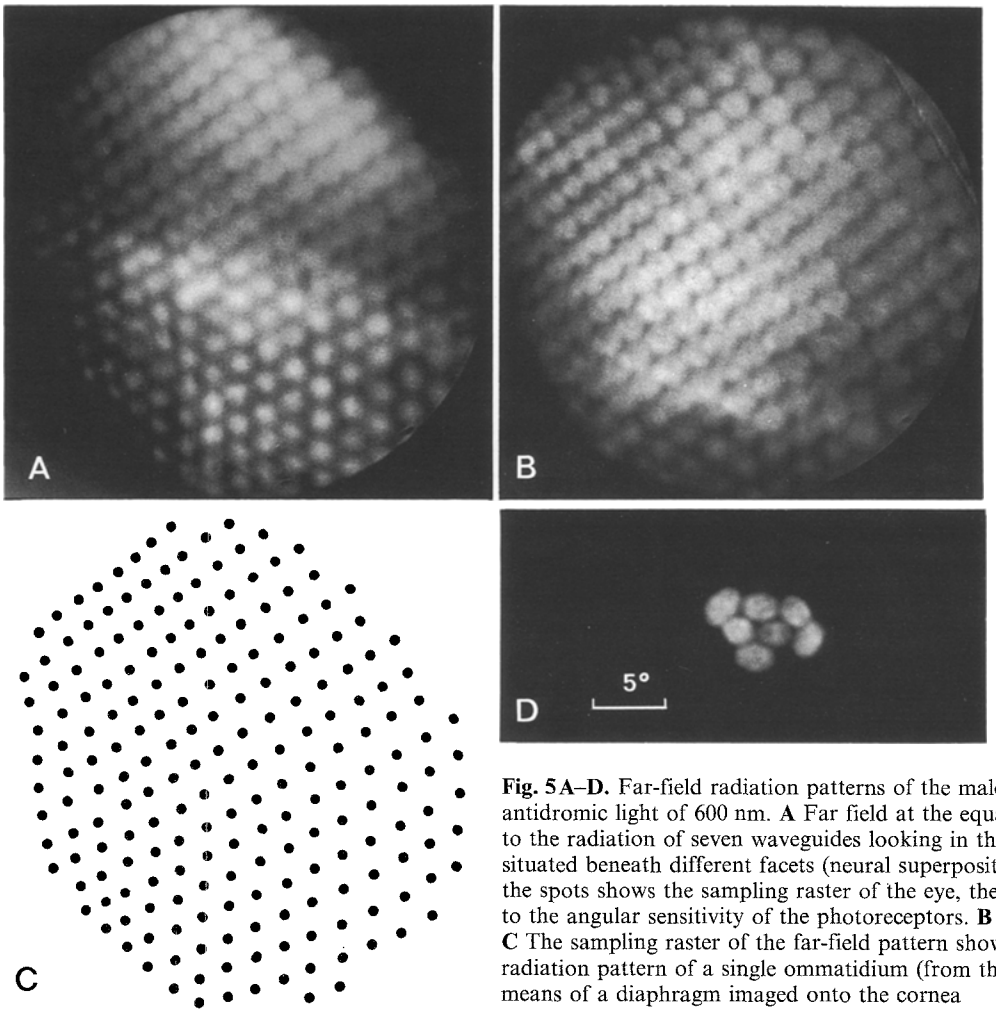


**Fig. 5A–D.** Far-field radiation patterns of the male dorsal eye, all viewed with antidromic light of 600 nm. **A** Far field at the equator. Each spot corresponds to the radiation of seven waveguides looking in the same direction, but situated beneath different facets (neural superposition). The distance between the spots shows the sampling raster of the eye, their intensity profile is related to the angular sensitivity of the photoreceptors. **B** As **A**, but more dorsally. **C** The sampling raster of the far-field pattern shown in **A. D** The far-field radiation pattern of a single ommatidium (from the centre of **B**), selected by means of a diaphragm imaged onto the cornea

gential sections of the dorsal eye was that the rhabdomeres taper very rapidly (Fig. 4A, B, C). Indeed, the proximal half of the retina appears to contain no rhabdomeres at all. The only exception is the rhabdomere of R8 which first appears near the basement membrane long after the other retinular cells, including the overlying R7, have ceased to produce a rhabdomere. In horizontal radial sections, it appeared that this marked tapering was confined to the area of large facets. In the lateral part of the dorsal eye where the facets are smaller, and below the equator, the rhabdomeres extend almost as far as the basement membrane.

In common with all other higher dipterans investigated so far (Wada 1974; rev. Hardie 1985), there is also a marginal zone of two or three rows of ommatidia in the dorsal eye where the central rhabdomeres R7 and R8 are greatly enlarged and presumably involved in the detection of polarized light.

*Observation of waveguide modes.* We recall that in the well-investigated fly species *Musca* and *Calliphora*, the rhabdomeres are about 2 μm in diameter (e.g. Horridge et al. 1976), and at long wavelengths can only support the first order waveguide mode – $LP_{01}$ (Franceschini 1975; Kirschfeld and Snyder 1976; van Hateren 1984). The same situation is encountered in the ventral eye of male *Chrysomyia* (Fig. 3A). With shorter wavelengths (e.g. 450 nm, see Fig. 3B) second order waveguide modes can be seen in ventral rhabdomeres, as is the case in rhabdomeres of *Calliphora* (van Hateren 1984, 1985) and in rhabdoms of butterflies (Nilsson et al. 1984, 1988). On the other hand, the wide rhabdomeres in the dorsal eye clearly show higher order waveguide modes even in light of 600 nm (Fig. 3A and, more dorsally, Fig. 3C), and still more complicated mode patterns with shorter wavelengths (Fig. 3B).

*Far-field radiation pattern.* What consequences does the increase in lens and rhabdomere diameter have for the resolving power of the eye (angular sensitivity and sampling raster)? A particularly useful technique for answering such questions is

the observation of the far-field radiation pattern of the antidromically illuminated eye (Franceschini 1975). Each blur circle in such a pattern represents the optical projection of a single sampling station (the superimposed image, at infinity, of seven aligned rhabdomeres) and thus its diameter is a measure of angular sensitivity whilst the separation of neighbouring points indicates the interommatidial angle. Figure 5 shows far fields at the equator (Fig. 5A), more dorsally (Fig. 5B), and the far-field radiation pattern of a single ommatidium (Fig. 5D). Figure 5A (schematized in Fig. 5C) shows that the sampling rasters are very similar ventrally and dorsally. The far-field radiation patterns of aligned rhabdomeres, though, are wider in the dorsal eye, and their intensity profile is not Gaussian-like as in the ventral eye (the ventral far-field patterns in Fig. 5A seem narrower than they really are due to the photography and reproduction). It should be appreciated that far-field radiation patterns are only equivalent to angular sensitivities for monomodal rhabdomeres (van Hateren 1984) as in the ventral eye. For multimodal rhabdomeres, as in the dorsal eye, the far-field radiation pattern is wider than the corresponding angular sensitivity because higher order modes are better transmitted and are thus seen more prominently than the lower order modes which are, however, preferentially absorbed. Below we will see that angular sensitivities of dorsal rhabdomeres are in fact approximately Gaussian as in the ventral rhabdomeres, and have half-widths comparable to those theoretically predicted for the monomodal ventral rhabdomeres (about 20% larger than the Airy diffraction limit of the lenses, see van Hateren 1984).

The conclusion is that both interommatidial angle and angular sensitivity remain virtually constant when crossing the equator, and there is no discontinuity in the way the eye samples its environment corresponding to the abrupt change in ommatidial dimensions. The main difference between the eye regions is that the larger facets provide a brighter retinal image and the photoreceptors in the specialized dorsal region are, all else being equal, more sensitive. Indeed, the far-field radiation pattern shows that the angles subtended by the enlarged dorsal rhabdomeres are about as great as the angle subtended by rhabdomeres in adjoining ventral eye regions. It follows that the receptor photon capture will approximately increase in proportion to facet area. Thus photoreceptors behind 80 μm dorsal facets will potentially be about 16 times more sensitive than photoreceptors underlying the 20 μm diameter ventral facets. Rather than an acute zone, we thus refer to the specialized dorsal eye region of male *Chrysomyia* as a 'bright zone'.

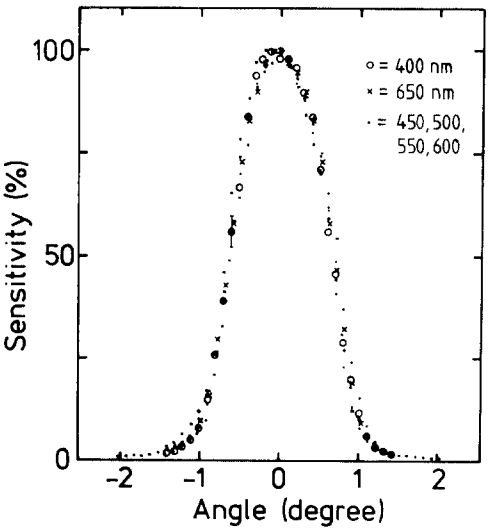


**Fig. 6.** Angular sensitivities measured electrophysiologically in an R2 for six different wavelengths. The facet diameter D = 65 μm (mean of inscribed and circumscribed circle of effective aperture), the half-width of the angular sensitivity $\Delta\rho = 1.37°$, and the interommatidial angle $\Delta\varphi = 1.4°$

Figure 5D is the far-field radiation pattern of a single ommatidium (also present in the centre of Fig. 5B). It shows again the higher order waveguide modes occurring dorsally at 600 nm, and when compared with Fig. 5B also shows that the eye is a neural superposition eye of the muscoid type, i.e. next neighbour rhabdomeres belong to next neighbour neuroommatidia (cf. the eye of Bibionidae, Zeil 1979, 1983a; rev. Land 1981a).

*Electrophysiology*

*Photoreceptor angular sensitivity.* Figure 6 shows the angular sensitivities measured electrophysiologically in a male dorsal R2 (optically identified in the far field). The data points of wavelengths 400 nm and 650 nm are shown as open circles and crosses respectively, the data points of the four other wavelengths (450, 500, 550, and 600 nm) are shown as small dots for clarity's sake. The error bar shown (typical measurement error) shows that the angular sensitivities are identical within the measurement error (see Discussion). The lens diameter was 65 μm, leading to diffraction limits of 0.35° at $\lambda = 400$ nm and 0.57° at $\lambda = 650$ nm. The measured $\Delta\rho$ (Fig. 6) was $1.37 \pm 0.04°$, thus much larger than the diffraction limit, as a consequence of the large dorsal rhabdomere diameters. From the far-field radiation pattern the interommatidial angle ($\Delta\varphi = 1.4°$) was found to be about the same

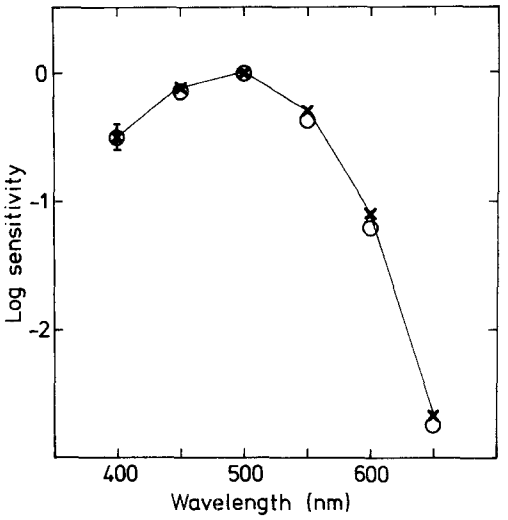


**Fig. 7.** Spectral sensitivities of an R2 and R4 (crosses), and an R7 (open circles) as measured in an LMC whilst illuminating only the R7. The different wavelengths were measured with Balzers K-filters. The UV could not be measured due to technical limitations of the setup used for microstimulation

as $\Delta\rho$. An equivalent measurement in an R4 of another animal yielded very similar results (identical angular sensitivities for 400, 500, and 600 nm, Gaussian-shaped with $\Delta\rho = 1.42 \pm 0.04°$; the lens diameter was 64 μm and $\Delta\varphi = 1.7°$).

*LMC responses.* By combining recording from the large monopolar cells (LMCs) with single rhabdomere stimulation (see van Hateren 1987) it is possible to determine which photoreceptors have inputs to the LMC, and also to determine the properties (e.g. spectral sensitivity) of the individual inputs. Experiments which would otherwise require recording from many photoreceptors combined with intracellular dye-injection, can thus be performed with a single recording.

Neural superposition was directly checked by recording from LMCs in the lamina, and stimulating individual photoreceptors in the far field. This was done by selecting single ommatidia in the area of recording by means of a diaphragm imaged onto a single facet (Riehle and Franceschini 1984; van Hateren 1984). The LMCs responded not only to stimulation of the peripheral rhabdomeres R1–R6, but equally well to stimulation of the central rhabdomere (consisting of R7 and R8) which would normally be expected to bypass the lamina (rev. Hardie 1985). The spectral sensitivity of an LMC when the central rhabdomere (R7/8) was stimulated (open circles in Fig. 7) was identical to the spectral sensitivity directly measured in an R2 and R4 (crosses in Fig. 7; the cells were optically identified in the far field). The UV-sensitivity could not be measured because the optical setup was not transparent enough to UV-light, but from the shape of the spectral sensitivity it seems likely that the visual pigment involved is similar to that found in R1–R6 of other dipterans (rev. Hardie 1985; Vogt 1987). The spectral sensitivity of R7 was confirmed by the response of its pupil (Franceschini 1975) to orthodromically applied stimulation of single photoreceptors (using corneal neutralization). Pupil closure was monitored through the reduction in the amount of antidromically transmitted light. This experiment showed that the pupil of R7 has the same absolute and spectral sensitivity as the pupil of R1–6.

## Discussion

The dorsal eye of the male *Chrysomyia* differs radically from the eyes of other known flies in having both enlarged lenses and enlarged photoreceptors. Whereas the rhabdomeres in the ventral region of the eye have dimensions similar to those of other Calliphoridae, those in the specialized dorsal region can be more than twice the diameter. The change from small to large rhabdomeres is abrupt and correlates with the change in facet diameter. Indeed, despite a large change in ommatidial dimensions at the border between the two eye regions, the spatial sampling parameters of the eye, i.e. the angular sensitivity and the interommatidial angle, are virtually unchanged. Thus in contrast with many other male dipterans (including *Musca, Calliphora* and hoverflies) where the enlarged dorsal facets are associated with higher acuity (Beersma et al. 1977), in male *Chrysomyia* the potential for high acuity is 'wasted' by the large rhabdomeres. This implies that the enlarged dorsal facets have evolved to provide a brighter retinal image, hence our description of this eye region as a bright zone. The increased sensitivity in this area may be important under conditions of low luminance or for tasks involving objects of low contrast (Kirschfeld and Wenk 1976; Snyder et al. 1977; Snyder 1979). Although large facets are used for increasing light capture in other animals (e.g. *Odontodactylus scyllarus*, Horridge 1977), this is as far as we know the first example of an eye where a large gradient in facet diameter is not accompanied by a corresponding gradient in interommatidial angle and/or angular sensitivity.

The sensitivity of the bright zone is further boosted by enlarging the central R7 rhabdomere and incorporating this cell into the neural superposition projection. A similar specialization was first described in the 'love-spot' region of the dorsal

retina in the male *Musca* (Franceschini et al. 1981; Hardie 1983) but otherwise has not been demonstrated in the corresponding region of other dipterans (rev. Hardie 1985). As in *Musca,* there is also the possibility that in *Chrysomyia* the observed binocular overlap between dorsal regions contributes to the enhancement of sensitivity.

### *The effect of rhabdomere geometry on performance*

The wide rhabdomeres of *Chrysomyia* result in an angular sensitivity almost four times as wide as the diffraction limit of the lenses. Thus diffraction is not a limiting factor, and the number of waveguide modes (for most wavelengths four or more) should, in principle, allow the rhabdomere's light-guiding behaviour to be described according to geometrical optics. The angular sensitivity of such a system should depend only on the aperture of the light guide and the focal length of the lens, and, in particular, should be independent of wavelength. This is exactly what we found (Fig. 6). However, Fig. 6 is not consistent with another prediction of geometrical optics: the angular sensitivity should be flat-topped, whereas the measured profile is more Gaussian-like than square. This contradiction, which seemed puzzling at first, can be resolved when we take into account the marked tapering of the rhabdomeres (Fig. 4).

The diffraction pattern falling on the rhabdomere aperture will excite different modes depending on its position. With on-axis illumination the diffraction pattern will mainly excite the lowest order mode $LP_{01}$. With off-axis illumination higher order modes like $LP_{11}$ and $LP_{21}$ will be excited more strongly (Smakman et al. 1984). These higher order modes are not propagated along the full length of the rhabdomere, but are cut-off due to the decreasing rhabdomere diameter (see e.g. Snyder 1975). Thus the higher the order of the mode, the less well it is absorbed by the tapered rhabdomere. Off-axis light is therefore less well absorbed than on-axis light, even if it is initially trapped by the rhabdomere. Qualitatively, at least, the tapering can thus account for the rounded shape of the angular sensitivities in Fig. 6.

Although rounding the angular sensitivity sacrifices some of the light, this may be worthwhile when one considers a likely task for the male eye: detecting, locating and tracking females. Flat-topped angular sensitivity functions introduce an element of uncertainty into the retinal image since small targets such as a female can move across the flat region of maximum sensitivity without generating a change in signal. Rounded angular sensitivities which overlap with neighbours provide for a better localization of points and edges by interpolation. In principle, discontinuities can be located with a resolution that is well below the limit associated with resolving two points, as in human hyperacuity tasks (rev. Westheimer 1981). The receptoral limits to hyperacuity are set by the effective noise level (photon capture), by the shapes of the angular sensitivity functions themselves, the accuracy with which these shapes are determined, the degree to which shape varies with respect to the wavelength of light, and the alignment of rhabdomeres within the superposition pattern. We suggest that in the dorsal eye the tapering of the rhabdomeres removes the ambiguities associated with flat-topped sensitivities and may also shape the angular sensitivity to a form that is well suited for locating and tracking moving objects.

As shown in Fig. 4 the tapering results in the proximal 50% of the retina actually becoming devoid of rhabdomeres in the bright zone. We can think of two factors which might explain why so much space should apparently be wasted: firstly, it is possible that there is a circadian rhythm whereby rhabdomeres extend over the whole depth of the retina during the night. However, measurements of antidromic transmission render this unlikely, as we could not detect any circadian change in transmission. Secondly, radial sections show that the shorter, strongly tapered rhabdomeres are restricted to the zone of large facets – the rest of the dorsal eye possesses longer rhabdomeres. Consequently, a distortion of the retina would occur if the ommatidia with tapering rhabdomeres were shortened.

The R8 cell, the rhabdomere of which appears in the depth of the retina with no contiguity to that of R7 (Fig. 4D) presumably has greatly reduced sensitivity and poor acuity. This resembles the situation in the *Musca* male dorsal eye, where although R8's rhabdomere is contiguous which that of R7, it contains the same visual pigment and its sensitivity is thus severely reduced by screening (Hardie et al. 1981). In both cases it would thus appear that the R8 cell may be vestigial in function. If this is so, to explain why the cell is still produced at all we note that R8 is believed to play a key role in the development of the entire ommatidium (rev. Wyman 1986).

### *Design principles*

In Fig. 8 we compare the geometry and performance of the conventional fly eye (Fig. 8A) with that of *Chrysomyia* (Fig. 8D), and examine hypo-

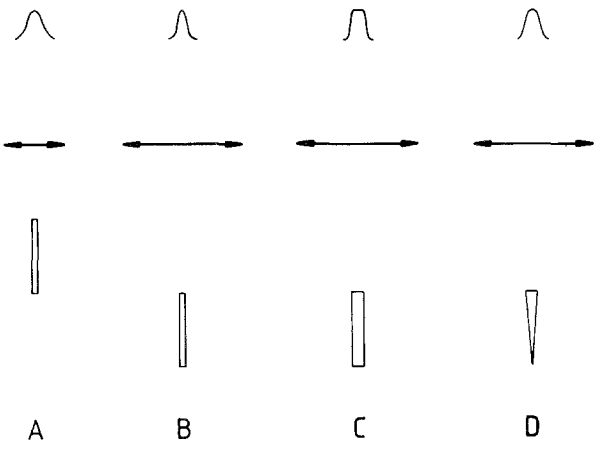


**Fig. 8A–D.** Design principles. **A** Conventional design; also the angular sensitivity is drawn. **B** The same rhabdomere, but a lens twice as large as in **A**. The angular sensitivity is now half that in **A**, and the photon capture for point sources four times that in **A**. **C** as **B**, but with increased rhabdomere diameter. The angular sensitivity has about the same half-width as in **A**, but has a square, flat-topped shape rather than a Gaussian one. **D** Tapering of the rhabdomere again leads to a Gaussian-shaped angular sensitivity. The design of **D** functions almost completely equivalent to the design of **A**, except that the light capture is about 4 times as large

thetical intermediates (Fig. 8B, C) in order to elucidate the design principles governing *Chrysomyia's* 'bright zone'.

The conventional eye combines a moderate size lens with a small rhabdom (Fig. 8A). The minimum usable size of the rhabdom (1–2 μm diameter) is constrained by the refractive index of the rhabdomere and the wavelength of light. These waveguide properties also determine the optimal F-number of the lens (van Hateren 1984, 1985). With an F-number between 2.0 and 2.5, 80% of incident light is trapped by the rhabdomere and the angular sensitivity of the system is only 15–20% broader than the diffraction limit of the lens (the Airy diffraction pattern). How might this basic design be modified to allow for the more efficient detection and tracking of small objects (females) by the dorsal region of a male eye?

The accuracy of detection and tracking is ultimately limited by the signal to noise ratios of photoreceptors. This ratio is set by the optical image quality and by photon noise. At all but the highest intensities, the effects of transducer noise, generated as the photoreceptors convert light to an electrical signal, is equivalent to a reduced photon capture (Lillywhite and Laughlin 1979; Howard and Snyder 1983; Howard et al. 1987). The fact that the male *Chrysomyia's* bright zone has large facets suggests that photon noise is a critical limiting factor for this animal. As discussed by Kirschfeld and Wenk (1976) and formulated quantitatively by Land (1981b), a photon noise limited receptor is better at detecting small dark objects against a background when the lens diameter is increased and the acceptance angle is decreased. The implementation of this strategy is illustrated in Fig. 8B. The lens diameter is doubled and, to keep the F-number at the same optimum value, so is the focal length. This reduces the angular subtense of the rhabdom and the angular size of the Airy diffraction pattern, so halving the acceptance angle.

If the number of ommatidia is kept constant, this increase in lens diameter raises a new problem – undersampling of the image. With such narrow angular sensitivities, the areas falling between receptive fields are not sampled with a high sensitivity. The problem of undersampling can be resolved in two ways. The first is to increase the number of ommatidia to provide an adequate coverage. Since this increase is combined with a larger lens, the eye radius increases as the square of facet diameter (Kirschfeld 1976), and larger optic lobes must be constructed to service more facets (Laughlin 1981). A more economical version is to increase the eye radius and facet diameter locally, to generate an acute zone (Collett and Land 1975; Horridge 1978) with high resolving power and light capture. The size of the eye and the number of ommatidia can only be held constant if facet diameters and eye radius are reduced in other eye regions. Thus the penalty for building this type of acute zone is the impoverishment of the image in other parts of the visual field.

A second strategy – and that which seems to have been adopted by *Chrysomyia* – is to maintain the original resolving power over the whole eye and to overcome the problem of undersampling in the region of enlarged facets by increasing the rhabdomere diameter (Fig. 8C). With wider rhabdomeres the angular sensitivity is expanded and the photon capture increased, though the photon capture for point sources remains the same. The imaging system is no longer diffraction-limited so the angular sensitivity profile assumes the shape of the rhabdomere aperture: i.e. it becomes squarer. As discussed above, the flat-topped sensitivity profile introduces ambiguity into the sampled image which reduces the accuracy with which small objects can be located and tracked. This ambiguity is removed by tapering the rhabdomeres (Fig. 8D) so as to generate an angular sensitivity profile that resembles that of the archetypical common eye (Fig. 8A). Since a photoreceptor's performance at detecting small objects improves with de-

creasing acceptance angle (Land 1981b; see above), *Chrysomyia's* strategy appears to be non-optimal. However, the probability of detecting a female will presumably depend on the volume of space that can be covered: in principle this can be increased both by enlarging the distance at which objects still can be detected, and by sampling a wider visual angle. If we assume that only a limited number of ommatidia can be devoted to this task, then in fact a larger volume of space can be monitored with larger interommatidial angles and broad angular sensitivities.

Lastly, let us consider the effect of the spectral sensitivity on the design of dorsal eye regions. Three of the most highly developed dorsal eyes to be described, namely the male bibionid, the male mayfly, and the male simuliid, are purely UV sensitive (Burkhardt and de la Motte 1972; Horridge and McLean 1978; Kirschfeld and Vogt 1986). UV sensitivity has two benefits whose relative efficacies have yet to be assessed. Firstly, UV sensitivity enhances the contrast of a target viewed against the scattered light of the sky (Mazokin-Porshniakov 1959). Secondly, the diameter of the Airy diffraction pattern decreases with wavelength. Consequently a diffraction-limited system forms a crisper image in the UV, again improving target contrast (Kirschfeld and Wenk 1976; Kirschfeld and Vogt 1986). The dorsal eye region of male *Chrysomyia* is so far from the diffraction limit that this latter advantage is irrelevant. The more conventional longer wave sensitivity of this retinal region raises two possibilities. Either the small gain in contrast that might accrue from UV sensitivity is more than compensated for by the increased photon capture, or the objects of interest to the male *Chrysomyia* are not usually silhouetted against the sky.

## Conclusions

The abundance and variety of male dorsal eye regions suggest that they have evolved independently on several occasions, even within the dipterans. Whilst it is a fair assumption that in each case they have evolved for the task of detecting and/or tracking females, the particular problems and the specific solutions can be expected to differ depending upon many factors such as the size, behaviour and habitat of each species. A proper understanding of the strategies involved requires a knowledge of all the relevant behavioural and ecological parameters. Unfortunately, too little is known about the behavioural ecology of *Chrysomyia*; the solution chosen by the males would suggest that light capture is at a premium, so we might predict that they either search for females under conditions of low luminance (e.g. under a canopy or at dawn and dusk), or are able to detect females at long distances under conditions of high luminance (see also Kirschfeld and Wenk 1976; Snyder et al. 1977).

One of the most striking consequences of the *Chrysomyia* strategy is that it allows for a relatively large part of the visual field having low photon noise, and thus higher accuracy, without the necessity of a greatly increased number of ommatidia and thus an enormous eye. As argued above this should increase the probability of detecting a female by increasing the volume of space that is covered. It is not possible to determine the optimum parameters for this strategy since other constraints are also involved. For example, there is little point in increasing the detection range ad infinitum because the maximum flight speed and manoeuvrability of the animal restrict the male's chances of catching a detected female (Kirschfeld and Wenk 1976). It is interesting to note that the bright zone in *Chrysomyia* actually contains approximately the same number of facets and covers about the same visual angle (ca. $30° \times 30°$) as the 'love spot' of the male *Musca* (Hardie 1983).

Apart from the obvious optical specializations of dorsal eyes there are also intriguing correlates to be found at various stages in the underlying visual ganglia. This has been best documented in the case of the male housefly (Hausen and Strausfeld 1980; Hardie 1983; rev. Hardie 1985) even though in this species the external sexual dimorphism in eye size is very modest. In particular, the axon of R7, which normally projects through to the medulla, joins the neural superposition scheme in making synapses with LMCs (Hardie 1983). Such a connection has been demonstrated electrophysiologically in the present study and it is of obvious interest now to examine whether the same or a different anatomical strategy has been employed. Shaw and Meinertzhagen (1986) and Shaw (1988) have demonstrated a high degree of conservatism in the neural circuitry of the dipteran lamina and, given the excellent neuroanatomical descriptions available, argue that this neuropil represents a valuable testing ground for ideas of how new neural circuits may have evolved. In this respect it would be of interest to examine in detail the synaptology of a variety of specialized male dorsal eyes.

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